A Decade of Predatory Control of Zooplankton Species Composition of Lake Michigan

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ABSTRACT. From 1983 to 1992, 71 species representing 38 genera from the Calanoida, Cladocera, Cyclopoida, Mysidacea, Rotifera, Mollusca and Harpacticoida comprised the offshore zooplankton community of Lake Michigan. Our data demonstrate that the composition and abundance of the calanoid community after 1983 is not unlike that of 1960s and that species diversity of the calanoid community is more diverse than the cladoceran community in the 1990s as compared to the early 1980s. Even though the relative biomass of the cladocerans has remained similar over the 1983–1993 period, the species diversity and evenness of the Cladocera community in the early 1990s is unlike anything that has been previously reported for Lake Michigan. Cladocera dominance is centered in one species, Daphnia galeata mendotae, *and only three species of Cladocera were observed in the pelagic region of the lake in 1991 and 1992. Nutrient levels, phytoplankton biomass, and the abundance of planktivorous alewife and bloater chub and* Bythotrephes *are examined as possible causes of these changes in zooplankton species composition. The increase in Rotifera biomass, but not Crustacea, was correlated with an increase in relative biomass of unicelluar algae. Food web models suggest* Bythotrephes *will cause Lake Michigan's plankton to return to a community similar to that of the 1970s; that is* Diaptomus *dominated. Such a change has occurred. However, correlational analysis suggest that alewife and bloater chubs (especially juveniles) are affecting size and biomass of larger species of zooplankton as well as* Bythotrephes.

INDEX WORDS: Lake Michigan, zooplankton biomass and population trends, food web, predation.

INTRODUCTION

Evidence of appreciable change in the biota of Lake Michigan (e.g., Jude and Tesar 1985, Evans and Jude 1986, Scavia et al. 1986, Fahnenstiel and Scavia 1987, Stewart and Ibarra 1991, Evans 1992) has directed attention to the long-term data sets of phytoplankton and zooplankton collected by the Great Lakes National Program Office of the U.S. Environmental Protection Agency. Phytoplankton, which have short carbon turnover rates, are sensitive to water quality conditions and grazing by zooplankton, and thus respond rapidly to perturbations of the lake ecosystem. The determination of phytoplankton abundance and species composition is one method to trace long-term changes in lakes (Munawar and Munawar 1982, Makarewicz 1993, Makarewicz and Bertram 1991). Similarly, whether aquatic ecosystems are perturbed by changes in the top predator fish that cascade down the food web or by nutrients or other stressors that are expressed from the first trophic level upward, the zooplankton are sensitive integrators of such changes (McNaught and Buzzard 1973). They have also proved useful for complementing phytoplankton data to assess the effects of water quality (Gannon and Stemberger

1978) and fish populations on biota (e.g., Brooks and Dodson 1965). Thus zooplankton have value as indicators of water quality and the structure of the biotic community. However, the large interannual variability in abundance of zooplankton requires long-term data sets to detect trends in zooplankton abundance (Evans 1992). Specifically, has there been a reduction or other change in the Lake Michigan zooplankton community concomitant with the top-down mediated changes observed in the planktivorous vertebrate fish and invertebrate community during the 1980s? In this study, the 1983–92 zooplankton data assemblages presented make it possible to examine the historical and seasonal relationships prevailing in Lake Michigan and to compare them, where possible, to previous studies.

METHODS

A Wildco Model 30-E28 conical style net (62-μm mesh net; D:L ratio = 1:3) with 0.5-m opening (radius = 0.25m) was used to collect a vertical zooplankton sample at the same stations (Fig. 1) at which phytoplankton were collected during 42 cruises from 1983 to 1992. Although other dates were occasionally sampled (e.g., February, October), samples were consistently sampled during the unstratified spring period (23 March to 6 June) and the stratified summer (August) period (Table 1). Vertical tows were taken from 20 m to the surface. Filtration volume was determined with a Kahl flow meter (Model 00SWA200) mounted 1/3 of the net diameter from one edge. Following collection, the net contents were quantitatively transferred to 500-mL sample bottles, narcotized with club soda, and preserved with 5% formalin.

Enumeration of zooplankton followed Gannon (1971) while identification followed Stemberger (1979) and Edmondson (1959). The volume of each rotifer species was computed by using the geometrical shape that most closely resembled the species (Downing and Rigler 1984). For each cruise, the length of at least 20 specimens of each rotifer species was measured. Width and depth were also measured on one date for each lake to develop length-width and length-depth ratios for use in the simplified formulas of Bottrell *et al.* (1976). Assuming a specific gravity of one, volume was converted to fresh weight and to dry weight assuming a ratio of dry to wet weight of 0.1 (Doohan 1973) for all rotifer species except *Asplanchna* spp. A dry weight/wet weight ratio of 0.039 was used for *Asplanchna* spp. (Dumont *et al.* 1975).
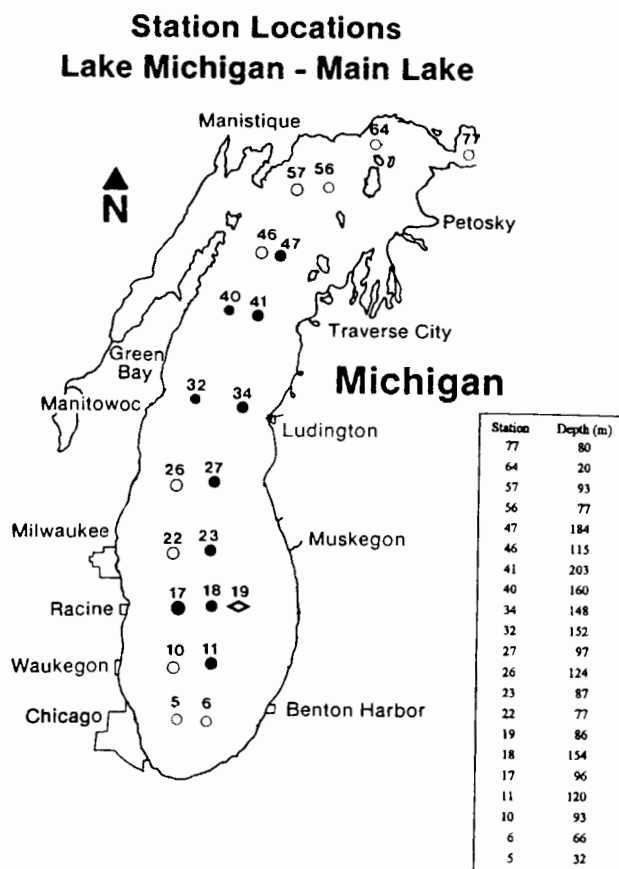
Station Locations
Lake Michigan - Main Lake

Station	Depth (m)
77	80
64	20
57	93
56	77
47	184
46	115
41	203
40	160
34	148
32	152
27	97
26	124
23	87
22	77
19	86
18	154
17	96
11	120
10	93
6	66
5	32

FIG. 1. Lake Michigan sampling stations, 1983–1992. ○ *= sampled only in 1983 and 1984.* ● *= sampled 1983–1982.* ◇ *= sampled in 1985–1992.*

Because of the considerable variability in length and thus weight encountered in the Crustacea, the dry weights of Crustacea were calculated using length-weight relationships (Downing and Rigler 1984, Makarewicz and Likens 1979). Average length of crustaceans (maximum of 20 for each station) was determined for each station of each cruise. A comparison of calculated weights to measured weights of individual Crustacea in Lake Michigan suggested good agreement at the minimum weight range (Makarewicz 1988). The weight of the Copepoda nauplii and the veliger of *Dreissena* followed Hawkins and Evans (1979) and Sprung (1993).

Statistical evaluations of zooplankton data and other data manipulations were conducted within the INFO data management system (Henco Software,

TABLE 1.   *Lake Michigan zooplankton sampling dates during the "unstratified spring" (March–June) and "stratified summer" (August only) periods from 1983 to 1992. Eleven stations were sampled on each date except where noted.*

Year	Unstratified Spring	Stratified Summer	Year	Unstratified Spring	Stratified Summer
1983	17–21 April 4–6 May	3–4 August 17–19 August	1988	31 March–2 April 21–24 April	4–6 August[3] 24–26 August
1984	9–12 April 6–7 May	1–3 August 12–14 August 15–16 August[1]	1989	23–24 March	7–9 August 26–28 August
1985	15–22 April 1–2 May	17–20 August	1990	29–31 March 4–6 April	2–4 August 21–23 August
1986	12–13 April 2–4 May	1–2 August 21–22 August	1991	28–29 March 23–24 April	20–22 August
1987	26–28 March[2] 13–14 April	21–24 August[2]	1992	16–20 April	18–23 August

[1] 24 stations sampled
[2] 10 stations sampled
[3] 12 stations sampled

Inc. 100 Fifth Avenue, Waltham, Mass.). Data from stations on a east west axis were averaged to give one point to allow north to south comparisons. All zooplankton identifications and enumerations were performed by the Bionetics Corporation (1983–88), AScI (1989,1990) and Enviroscience (1991–92).

Bloaters and alewife were collected during the fall by daytime 10-minute bottom trawls. Abundance estimates represent the mean number of fish caught at nine depths (i.e., 9 to 91 m at depth intervals of about 9 m) at each of seven index stations—Manistique, Frankfort, Ludington, and Saugatuck, Michigan; Waukegan, Illinois; and Sturgeon Bay, Wisconsin. These stations have been sampled consistently each year since 1973 to the present. Estimates of forage-fish biomass available to bottom trawls in 1992 are based upon catches at the seven index stations plus two new ones—Two Rivers, Wisconsin (added in 1990) and Little Traverse Bay (added in 1988). Further information on methodology for these fish surveys are presented in Brown *et al.* (1993). It is important to note that the fish trawls are estimates of abundance in the lower 1.8 m of the water column. Generally, significant differences were determined by oneway analysis of variance

and Tukey's Honestly Significant Difference (HSD) test (Dowdy and Wearden 1983).

RESULTS AND DISCUSSION

Mean Annual Abundance and Biomass of Zooplankton Groups

From 1983 to 1992, 71 species representing 38 genera from the Calanoida, Cladocera, Cyclopoida, Mysidacea, Rotifera, Mollusca, and Harpacticoida comprised the offshore zooplankton community of Lake Michigan. Twenty-one common species plus their juvenile stages accounted for 94.9% of the total biomass and 95.5% of the total abundance (Table 2) over the 10-year study period. Common species for each year of the study are presented in Makarewicz *et al.* (1995). The Rotifera contained the largest number of species (34) and accounted for the highest relative abundance (68.8%, Table 2). The Calanoida, Cyclopoida, and the copepod nauplii represented 25.2% of the total zooplankton abundance (Table 2). The Calanoida (34.4%) followed by the Cladocera (27.7%) and the Cyclopoida (15.1%) contributed the most biomass to the zooplankton community, while the Rotifera rep-

TABLE 2. **Summary of common zooplankton species occurrence in Lake Michigan during the unstratified spring period and the summer stratified (August only) period from 1983 to 1992. Species were arbitrarily classified as common if they accounted for ≥ 0.1% of the total abundance or ≥ 1.0% of the total biomass, with the exception of rotifers. Rotifer species were considered common if they accounted for ≥ 1.0% of the total abundance. The mean is calculated from all samples taken during the 1983–1992 period.**

Taxon	Maximum Density ($\#/m^3$)	Average Density ($\#/m^3$)	% of Total Abundance	Mean Biomass ($\mu g/m^3$)	% of Total Biomass
Copepoda					
Copepoda - nauplii	76,273	14,106	15.44	5,196	11.98
Cyclopoida					
Cyclopoid - copepodite	24,480	1,715	1.88	3,445	7.94
Cyclops bicuspidatus thomasi	14,688	731	0.80	2,924	6.74
Tropocyclops prasinus mexicanus	2,893	95	0.10	186	0.43
Calanoida					
Diaptomus - copepodite	50,741	4,071	4.45	7,791	17.96
Diaptomus ashlandi	9,352	1,412	1.55	3,508	8.09
Diaptomus minutus	11,873	595	0.65	1,410	3.25
Diaptomus sicilis	2,395	268	0.29	1,535	3.54
Limnocalanus macrurus	1,725	47	0.05	694	1.60
Total			25.22		61.52
Cladocera					
Bosmina longirostris	21,216	261	0.29	439	1.01
Daphnia galeata mendotae	43,288	1,032	1.13	9,841	22.68
Daphnia pulicaria	6,056	102	0.11	746	1.72
Holopedium gibberum	1,318	7	0.01	997	2.30
Total			1.53		27.71
Rotifera					
Collotheca sp.	15,401	1,119	1.22	4	0.01
Conochilus unicornis	376,238	13,514	14.80	188	0.43
Gastropus stylifer	21,698	1,745	1.91	47	0.11
Kellicottia longispina	42,745	3,094	3.39	376	0.87
Keratella cochlearis	234,866	13,409	14.68	74	0.17
Keratella crassa	64,602	3,774	4.13	294	0.68
Ploesoma truncatum	69,895	2,610	2.86	76	0.18
Polyarthra major	53,757	1,826	2.00	393	0.91
Polyarthra remata	22,857	1,098	1.20	19	0.04
Polyarthra vulgaris	467,205	13,136	14.38	743	1.71
Synchaeta sp.	98,070	7,469	8.18	229	0.53
Total			68.75		5.63
Total			95.51		94.85

resented only 5.6% of the zooplankton biomass over the 10-year period. Average density and biomass for 1983 –1992 (unstratified spring and stratified summer) (August only) was 91.3 organisms/L ± 6.7 (mean ± S.E.) and 48.0 µg/L ± 4.3 (mean ± S.E.). Biomass was considerably higher in the summer (81.8 ± 8.5 µg/L) than in the spring period of sampling (20.1 ± 1.6 µg/L) (Tables 3 and 4). In comparison to lakes worldwide, a mean biomass of 48 µg/L ranks in the range of biomass for oligotrophic and mesotrophic lakes (Schindler and Noven 1971).

Some time-trend patterns in biomass do emerge. The relative importance of the Cladocera varied over the study period (Fig. 2). Relative biomass of Cladocera (unstratified spring and stratified summer

TABLE 3. Zooplankton biomass and abundance of major groups in Lake Michigan, 1983–1992 (March to June). ND = no data, ** weighted mean that considers the number of stations sampled each year. A = Unstratified Spring Biomass. B = Unstratified Spring Abundance.

Year	Calanoida μg/L	%	Cladocera μg/L	%	Copepoda Nauplii μg/L	%	Cyclopoida μg/L	%	Rotifera μg/L	%	Mean μg/L
A											
1983	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
1984	3.6	43.8	0.002	<0.1	3.4	41.4	1.1	12.9	0.137	1.7	8.2
1985	27.4	74.8	0.052	<0.1	7.0	19.2	2.0	5.4	0.111	0.3	36.6
1986	10.4	49.0	0.018	<0.1	7.3	34.3	3.4	16.1	0.115	0.5	21.2
1987	9.9	54.3	0.003	<0.1	5.3	28.8	3.0	16.6	0.060	0.3	18.3
1988	8.2	54.7	0.003	<0.1	4.3	28.8	2.4	15.7	0.116	0.8	15.0
1989	10.0	65.2	0.001	<0.1	3.5	23.1	1.7	11.0	0.106	0.7	15.3
1990	9.4	65.9	0.0003	<0.1	3.6	25.0	1.2	8.7	0.015	0.1	14.3
1991	9.1	58.4	0.000	<0.1	5.3	34.1	1.1	6.9	0.029	0.2	15.6
1992	12.9	61.9	0.020	<0.1	5.0	24.2	2.3	10.9	0.580	2.8	20.8
1983–92	11.9	62.7	0.013	<0.1	5.0	26.2	2.0	10.3	0.106	0.6	20.1**
B	#/L	%	#/L	%	#/L	%	#/L	%	#/L	%	#/L
1983	6.8	26.5	0.017	<0.1	14.3	55.7	0.5	1.8	4.1	16.0	25.7
1984	1.2	7.5	0.001	<0.1	8.5	51.2	0.5	3.1	6.4	38.2	16.7
1985	4.6	17.5	0.010	<0.1	17.6	66.7	0.9	3.2	3.3	12.6	26.4
1986	3.6	13.7	0.002	<0.1	18.2	68.2	0.7	2.5	4.1	15.6	26.7
1987	3.8	18.8	0.002	<0.1	13.2	64.6	1.1	5.3	2.3	11.4	20.4
1988	3.3	16.9	0.001	<0.1	10.8	54.9	0.9	4.7	4.6	23.4	19.6
1989	3.0	17.0	0.001	<0.1	8.9	51.0	0.8	4.5	4.8	27.5	17.4
1990	2.9	22.2	0.0001	<0.1	8.9	68.7	0.5	3.5	0.7	5.6	13.0
1991	3.7	20.7	0.000	<0.1	13.3	73.8	0.6	3.4	0.4	2.1	18.0
1992	5.7	26.9	0.002	<0.1	12.6	59.5	0.8	3.7	2.1	9.9	21.2
1983–92	4.2	18.7	0.005	<0.1	14.0	62.9	0.8	3.4	3.3	15.0	21.1**

(August only)) was 45.3% in 1984, decreased to approximately 20% from 1985–91 with a low of 8.5% in 1987, and increased dramatically to over 50% of the total zooplankton biomass in 1991 and 1992. Summer Cladocera biomass varied even more, decreasing from 41.7 μg/L in 1984 to a low of 6.4 μg/L in 1987, and then peaking at 92.9 μg/L in 1991 (Table 3). An inverse correlation ($r = -0.83$) between Calanoida and Cladocera relative biomass was observed (Fig. 2). Relative biomass (unstratified spring and stratified summer (August only)) of the Cyclopoida was highest in 1986 (33%) and lowest in 1991–92 (< 5.5%). Rotifer relative biomass was low (<2%) through 1986 then it peaked at 15% in 1987, decreased steadily through 1990 and then increased again to a 1992 peak of about 20% of the total biomass (Fig. 2). Much of this later increase was due to *Asplanchna priodonta* in 1991 and to *Kellicottia longispina* and *Polyarthra vulgaris* in 1992. With the exception of 1991, rotifer abundance increased by at least a factor of two after 1986 compared to the 1983–1986 period.

The geographical pattern of total zooplankton biomass in Lake Michigan varied little over the study period (Fig. 3), with the exception of August of 1992. A peak at Station 11 in the southern basin in August of 1992 was due to a pulse of *Daphnia galeata mendotae* (25 organisms/L). Although biomass appeared to be lower at Stations 77, 64, 57, and 6, all nearer shore or in shallower waters than the deep water sites, no conclusions can be drawn on geographical differences because the difference is insignificant and because Stations 77, 64, 57, and 6 were sampled in only 1 year.

Planktivorous Fish

Relative abundance of adult and young-of-the-year alewife (*Alosa pseudoharengus*) and bloater (*Coregonus hoyi*) are presented in Figures 4 and 5.

TABLE 4. *Zooplankton biomass and abundance of major groups in Lake Michigan, 1983–1992 (August data only). ND = no data, ** weighted mean that considers the number of stations sampled each year. A = Unstratified Spring Biomass. B = Unstratified Spring Abundance.*

Year	Calanoida µg/L	%	Cladocera µg/L	%	Copepoda Nauplii µg/L	%	Cyclopoida µg/L	%	Rotifera µg/L	%	Mean µg/L
A											
1983	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
1984	21.1	25.4	41.7	50.1	6.6	7.9	11.9	14.3	1.9	2.3	83.3
1985	27.2	37.1	31.7	43.2	5.0	6.9	6.7	9.2	2.7	3.6	73.3
1986	53.9	35.3	36.0	23.6	7.8	5.1	54.0	35.4	1.1	0.7	152.7
1987	10.5	26.6	6.4	16.4	5.8	14.7	5.4	13.7	11.3	28.6	39.3
1988	14.9	37.9	8.3	21.0	4.9	12.5	6.2	15.8	4.8	12.2	39.4
1989	8.8	35.0	7.6	30.2	3.6	14.1	2.5	9.9	2.5	9.8	25.1
1990	27.2	40.1	18.5	27.3	6.9	10.2	10.4	15.3	4.7	7.0	67.8
1991	17.7	12.9	88.9	64.9	9.2	6.7	4.9	3.6	15.2	11.1	137.0
1992	18.3	11.1	92.9	56.5	9.4	5.7	7.9	4.7	35.9	21.8	164.5
1983–92	20.0	28.5	26.6	37.8	5.4	7.7	12.0	17.1	6.1	8.7	81.8**
B	#/L	%	#/L	%	#/L	%	#/L	%	#/L	%	#/L
1983	5.2	5.7	2.1	2.3	7.5	8.3	2.3	2.6	73.7	81.1	90.8
1984	10.3	8.2	4.7	3.7	16.5	13.1	6.1	4.8	88.5	70.2	126.1
1985	4.8	5.5	3.3	3.8	12.6	14.6	3.8	4.4	61.9	71.7	86.4
1986	18.8	16.7	3.9	3.5	19.4	17.2	10.6	9.4	60.2	53.3	113.0
1987	8.3	4.8	5.6	3.2	14.4	8.4	4.2	2.4	140.2	81.2	172.7
1988	7.5	3.4	1.9	0.8	12.3	5.5	4.0	1.8	196.9	88.5	222.5
1989	5.2	3.4	1.4	0.9	8.9	5.9	2.2	1.4	134.1	88.3	151.8
1990	12.8	4.6	2.0	0.7	17.3	6.2	4.8	1.7	243.4	86.8	280.6
1991	9.6	7.2	5.8	4.4	23.1	17.3	4.2	3.1	90.9	68.0	133.7
1992	12.1	3.2	7.4	1.9	23.5	6.2	6.6	1.7	329.7	86.9	379.4
1983–92	9.2	5.5	3.2	1.9	14.2	8.5	4.7	2.8	136.0	81.3	178.8**

Adult bloater relative abundance increased in the early 1980s and remained high through 1992. Adult (age 1+) alewife relative abundance was low from 1983 to 1985 compared to the 1970s and was relatively high in 1986, 1987, 1989 and 1990 compared to 1983–1985.

Correlations Between Planktivores and Zooplankton

For the entire 1983–92 period, strong negative correlations existed between *Daphnia pulicaria* biomass and abundance of *Bythotrephes* (r = –1.0), adult bloater (–0.84), and adult and juvenile alewife (r = –0.94, –0.96)(Table 5). Weaker negative correlations were observed between adult and juvenile alewife abundance and *Daphnia retrocurva* biomass (–0.63, –0.62) and *Bythotrephes* and biomass of *Holopedium gibberum* (–0.62), *Leptodora kindtii* (–0.75), and *Mesocyclops edax* (–0.63). Similarly,

negative correlations (r > –0.5) existed between *Leptodora kindtii* length and *Bythotrephes* abundance and between *Daphnia retrocurva, D. g. mendotae, H. gibberum, E. lacustris,* and *M. edax* length and alewife abundance (juveniles and adults) (Table 6).

In the 1983–86 period, a period of relaxed alewife predation with *Bythotrephes* not present in the lake, there were no strong negative correlations (r > –0.5) between alewife and the zooplankton biomass and length grouped as Cyclopoida, Calanoida, and Cladocera, except for Calanoida length (Table 7). Alewife abundance (adults and juveniles) was inversely correlated (r > –0.67) with length of all species of *Diaptomus, Epischura lacustris, Mesocyclops edax* and *Cyclops bicuspidatus thomasi* and was negatively correlated with biomass of *Daphnia,* especially *Daphnia pulicaria, Leptodora kindtii, Diaptomus sicilis, Limnocalanus macrurus* and *M. edax* (Table 5 and 6).
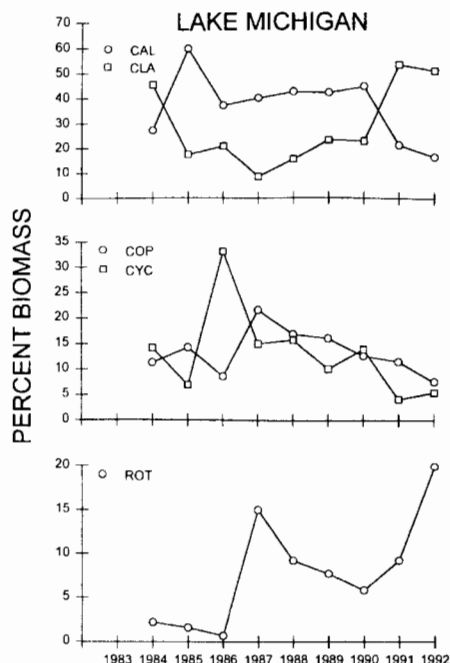
FIG. 2. *Yearly trends (unstratified spring and stratified summer (August only)) in relative biomass of selected groups of zooplankton, 1983–1992. CLA = Cladocera, CYC = Cyclopoida (adults and copepodites), CAL = Calanoida (adults and copepodites), ROT = Rotifera, COP = Copepoda Nauplii.*

FIG. 3. *Geographical distribution of zooplankton biomass (dry weight) in Lake Michigan, 1983–92. Values are the mean ± S.E. Area A and B represents stations sampled only in 1984.*

High negative correlations (r > –0.62) existed between bloater (adult and juvenile) and Cyclopoida and Calanoida biomass and Cladocera length during the 1983–86 period (Table 7). Adult bloater abundance was negatively correlated (r > –0.60) with length of *Daphnia galeata mentodae, Leptodora kindtii, B. longirostris,* and *Limnocalanus macrurus* while only juvenile bloater was strongly correlated with *D. g. mendotae* length (r = –0.79) (Table 6). Adult and occasionally juvenile bloater abundance was negatively correlated (r > –0.62) with biomass of *Holopedium gibberum, Bosmina longirostris, Diaptomus ashlandi, D. minutus,* and *Cyclops bicuspidatus thomasi* (Table 5).

During the 1987–92 period, alewife and bloater abundance increased and *Bythotrephes* appeared in the water column. Negative correlations (r > –0.50) existed between adult and juvenile alewife and the average length and biomass of Cladocera (Table 7) and between juvenile bloater and Cladocera bio-
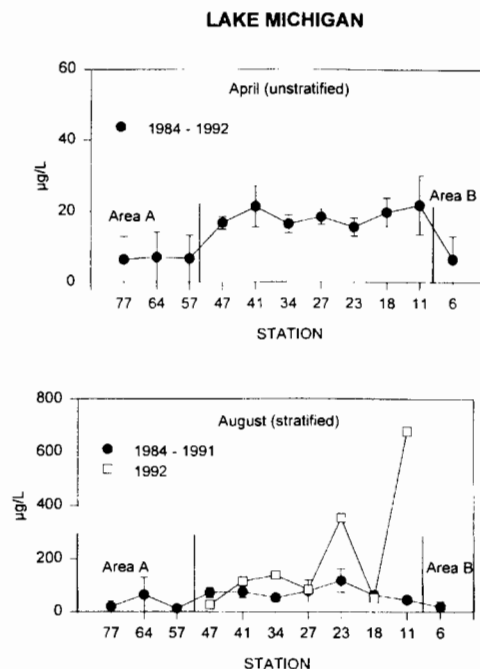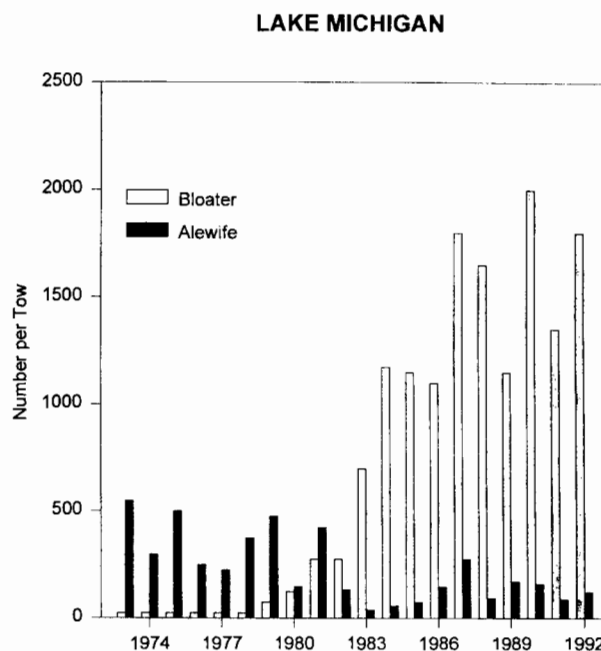

FIG. 4. *Annual relative abundance (catch per unit effort) of adult (age 1+)* Coregonus hoyi *and* Alosa pseudoharengus. *Data from Brown* et al. *(1993).*
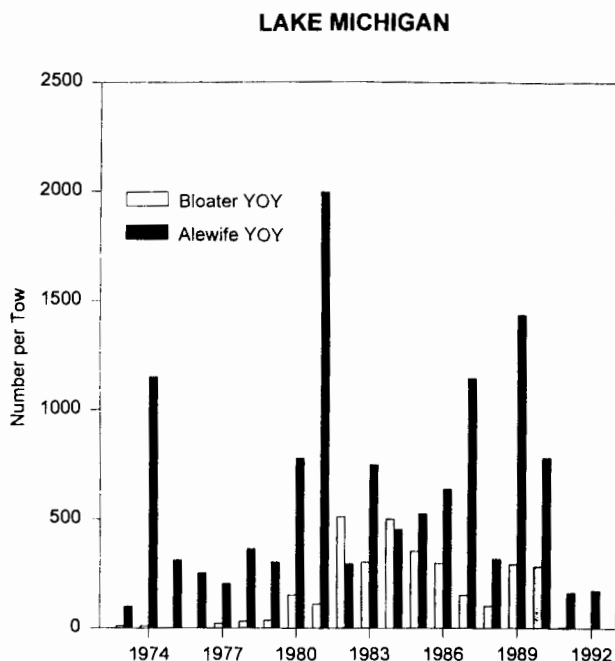
LAKE MICHIGAN

FIG. 5. Annual relative abundance (catch per unit effort) of young-of-the-year **Coregonus hoyi** *and* **Alosa pseudoharengus.** *Data from Brown* et al. *(1993).*

mass and length. Specifically, high negative correlations ($r > -0.62$) existed between alewife (adult and juvenile abundance) and the lengths of the larger Cladocera, Calanoida, and Cyclopoida (*Leptodora kindtii, Daphnia galeata mendotae, D. retrocurva, Limnocalanus macrurus, Epischura lacustris*, and *Mesocyclops edax*) (Table 6). Relatively high negative correlations ($r > -0.50$) between zooplankton length and adult bloater and *Bythotrephes* were not evident except for *L. kindtii* and *Bythotrephes* abundance. Juvenile bloater abundance was inversely correlated ($r > -0.66$) with length of *H. gibberum, L. kindtii*, and *E. lacustris*. In general, inverse correlations did not exist between zooplankton biomass and alewife, bloater or *Bythotrephes* abundance with the exception of *Daphnia galeata mendotae, D. minutus*, and *D. sicilis* with juvenile alewife ($r > -0.57$) and with juvenile bloater ($r > -0.64$) (Table 5) and *D. sicilis* and *D.galeata mendotae* with adult alewife ($r > -0.50$).

During the 1990–92 period, strong negative correlations ($r > -0.98$) were observed between abundance of planktivorous predators (adult and juvenile alewives and bloater and *Bythotrephes*) and Cladocera length and abundance (Table 7). Within the Cladocera, only the biomass of *D. galeata mendotae* was negatively correlated with abundance of the three predators (Table 5). Although the Calanoida as a group were not negatively correlated with the three planktivorous predators, biomass of *Diaptomus minutus* and *D. sicilis*, and length of the large *Epischura lacustris* and *Limnocalanus macrurus* were (Table 5 and 6).

Historical Trends in Biomass

Crustacean studies of the offshore waters of the Lake Michigan basin are few in number. Offshore crustacean zooplankton biomass data are available from 1976 (Bartone and Schelske 1982) for northern Lake Michigan. No information is presented on sampling intensity or technique. A comparison with the average lakewide 1984 and 1985 biomass data (Table 8) revealed that no significant difference in crustacean biomass existed between 1976 and 1984 and 1985. Another longer sequence of data from July and August collections are described by Scavia *et al.* (1986). Except for 1977, 1983, and 1984, zooplankton samples were primarily from an offshore station (40–m depth) west of Benton Harbor, Michigan. Zooplankton samples in the above three years were collected at an offshore station (100-m depth) west of Grand Haven, Michigan. A comparison of the 1984 mean offshore lake-wide biomass data to Scavia's data indicated good agreement (Fig. 6), thereby adding some confidence to comparisons between the data sets.

Within the 1983–92 data set, the 1986 and 1992 mean August biomass were significantly higher (P < 0.05, Tukey Test) than the 1987–89 biomass. The high 1986 and 1992 zooplankton biomass do not appear to be greatly different from the 1981 and possibly the 1978 data of Scavia *et al.* (1986) (Fig. 6). From 1974 through 1989, there were no obvious trends in zooplankton biomass, except that a peak in biomass occurred every 3 to 5 years. After 1989, zooplankton biomass progressively increased to a peak in 1992 (Fig. 6).

Historical Changes in Species Composition

Rotifera

Rotifer studies reported in the literature are primarily from the nearshore region of the lake. The abundance of rotifers in Lake Michigan has generally decreased from the nearshore into the offshore

TABLE 5. *Correlation* (*r*) *between alewife, bloater, and* **Bythotrephes** *abundances and biomass of selected species of zooplankton (August only). Adults = age 1+. YOY = Young of Year. NA means that the organism was absent.*

	1983–92		1983–86		1987–92		1990–92	
	Adults	YOY	Adults	YOY	Adults	YOY	Adults	YOY
Alewife								
Bosmina longirostris	0.81	0.48	0.97	0.90	0.80	0.46	0.89	1.00
Daphnia galeata mendotae	−0.33	−0.64	−0.48	−0.66	−0.53	−0.71	−0.85	−1.00
Daphnia pulicaria	−0.94	−0.96	−0.95	−0.86	0.06	0.10	0.87	1.00
Daphnia retrocurva	−0.63	−0.62	−0.43	−0.62	0.14	0.21	0.87	1.00
Holopedium gibberum	0.23	−0.20	0.98	0.92	0.06	0.12	0.87	1.00
Leptodora kindtii	−0.55	−0.39	−0.75	−0.88	0.75	0.35	NA	NA
Diaptomus ashlandi	0.15	0.07	0.82	0.68	0.12	0.09	0.84	1.00
Diaptomus minutus	0.05	−0.39	0.98	0.92	−0.33	−0.57	−1.00	−0.92
Diaptomus sicilis	−0.37	−0.59	−0.53	−0.70	−0.54	−0.68	−0.89	−1.00
Limnocalanus macrurus	−0.39	−0.20	−0.64	−0.78	−0.27	−0.18	−0.16	0.32
Epischura lacustris	0.60	0.23	−0.32	-0.52	0.50	0.18	0.90	1.00
Cyclops bicuspidatus thomasi	−0.04	−0.11	0.74	0.58	0.09	−0.15	0.99	0.94
Mesocyclops edax	−0.48	−0.46	−0.63	−0.79	0.87	0.49	NA	NA
Bloater								
Bosmina longirostris	0.59	0.04	−0.92	−0.66	0.60	0.44	1.00	1.00
Daphnia galeata mendotae	−0.08	−0.59	0.62	0.90	−0.21	−0.77	−0.99	−1.00
Daphnia pulicaria	−0.84	0.71	0.89	0.60	0.98	0.55	0.99	1.00
Daphnia retrocurva	−0.34	0.84	0.57	0.87	0.97	0.63	0.99	1.00
Holopedium gibberum	−0.27	−0.27	−0.94	−0.70	0.98	0.56	0.99	1.00
Leptodora kindtii	−0.32	0.81	0.85	0.99	−0.18	0.03	NA	NA
Diaptomus ashlandi	0.49	0.30	−0.72	−0.34	0.91	0.42	0.96	0.99
Diaptomus minutus	−0.02	−0.68	−0.94	−0.71	−0.18	−0.70	−0.95	−0.90
Diaptomus sicilis	0.09	−0.40	0.66	0.92	−0.01	−0.64	−1.00	−1.00
Limnocalanus macrurus	0.14	0.41	0.75	0.96	0.43	0.04	0.23	0.35
Epischura lacustris	0.81	−0.36	0.47	0.81	0.82	0.31	1.00	1.00
Cyclops bicuspidatus thomasi	0.12	0.40	−0.62	−0.22	0.84	0.11	0.97	0.93
Mesocyclops edax	−0.48	0.84	0.75	0.96	−0.18	0.10	NA	NA
Bythotrephes								
Bosmina longirostris	0.41		NA		0.46		1.00	
Daphnia galeata mendotae	−0.05		NA		−0.12		−0.99	
Daphnia pulicaria	−1.00		NA		0.98		0.99	
Daphnia retrocurva	−0.41		NA		0.98		0.99	
Holopedium gibberum	−0.62		NA		0.98		0.99	
Leptodora kindtii	−0.75		NA		−0.39		NA	
Diaptomus ashlandi	0.52		NA		0.95		0.96	
Diaptomus minutus	−0.13		NA		−0.11		−0.95	
Diaptomus sicilis	0.17		NA		0.10		−1.00	
Limnocalanus macrurus	0.56		NA		0.51		0.23	
Epischura lacustris	0.75		NA		0.74		1.00	
Cyclops bicuspidatus thomasi	0.16		NA		0.84		0.97	
Mesocyclops edax	−0.63		NA		−0.35		NA	

TABLE 6. *Correlation (r) between alewife, bloater, and* **Bythotrephes** *abundances and length of selected species of zooplankton (August only). Adults = age 1+. YOY = Young of Year. NA means that the organism was absent.*

	1983–92		1983–86		1987–92		1990–92	
	Adults	YOY	Adults	YOY	Adults	YOY	Adults	YOY
Alewife								
Bosmina longirostris	−0.11	−0.38	1.00	0.97	−0.48	−0.53	1.00	0.92
Daphnia galeata mendotae	−0.47	−0.56	1.00	0.96	−0.62	−0.58	0.24	0.67
Daphnia pulicaria	0.69	0.85	0.34	0.13	NA	NA	NA	NA
Daphnia retrocurva	−0.53	−0.69	0.52	0.33	−0.68	−0.83	NA	NA
Holopedium gibberum	−0.48	−0.57	−0.09	0.13	NA	NA	NA	NA
Leptodora kindtii	−0.79	−0.93	0.89	0.77	−0.79	−0.98	NA	NA
Diaptomus ashlandi	−0.07	0.20	−0.99	−1.00	−0.13	0.22	1.00	0.83
Diaptomus minutus	−0.29	0.19	−0.94	−0.99	−0.26	0.23	0.99	0.93
Diaptomus sicilis	−0.18	−0.02	−0.94	−0.99	−0.24	−0.03	0.71	0.29
Epischura lacustris	−0.55	−0.75	−0.82	−0.67	−0.67	−0.78	−0.63	−0.92
Limnocalanus macrurus	−0.16	−0.33	0.72	0.55	−0.52	−0.45	−0.92	−0.62
Cyclops bicuspidatus thomasi	0.84	0.65	−0.94	−0.99	0.93	0.68	0.99	0.80
Mesocyclops edax	−0.94	−0.71	−0.96	−1.00	−1.00	−0.66	NA	NA
Bloater								
Bosmina longirostris	0.65	−0.28	−0.98	0.81	0.74	−0.07	0.96	0.91
Daphnia galeata mendotae	0.40	−0.15	−0.98	−0.79	0.47	−0.24	0.59	0.69
Daphnia pulicaria	0.99	−0.47	−0.19	0.26	NA	NA	NA	NA
Daphnia retrocurva	0.50	0.48	−0.38	0.06	0.96	0.55	NA	NA
Holopedium gibberum	−0.10	−0.03	−0.07	−0.49	1.00	−1.00	NA	NA
Leptodora kindtii	−0.37	0.34	−0.81	−0.47	0.36	−0.75	NA	NA
Diaptomus ashlandi	0.64	0.20	1.00	0.90	0.63	0.62	0.88	0.81
Diaptomus minutus	0.46	0.43	0.98	0.97	0.50	0.65	0.96	0.92
Diaptomus sicilis	0.39	−0.04	0.98	0.97	0.35	0.21	0.38	0.27
Epischura lacustris	0.08	−0.44	0.71	0.34	0.04	−0.66	−0.88	−0.93
Limnocalanus macrurus	−0.04	−0.45	−0.60	−0.19	−0.24	−0.29	−0.70	−0.60
Cyclops bicuspidatus thomasi	0.23	−0.06	0.98	0.97	0.07	0.42	0.86	0.78
Mesocyclops edax	−0.41	0.33	0.99	0.94	−0.30	−0.17	NA	NA
Bythotrephes								
Bosmina longirostris	0.65		NA		0.78		0.96	
Daphnia galeata mendotae	0.52		NA		0.58		0.59	
Daphnia pulicaria	1.00		NA		NA		NA	
Daphnia retrocurva	0.63		NA		1.00		NA	
Holopedium gibberum	0.17		NA		1.00		NA	
Leptodora kindtii	−0.77		NA		−0.66		NA	
Diaptomus ashlandi	0.76		NA		0.74		0.88	
Diaptomus minutus	0.67		NA		0.64		0.96	
Diaptomus sicilis	0.55		NA		0.51		0.38	
Epischura lacustris	0.18		NA		0.13		−0.88	
Limnocalanus macrurus	−0.31		NA		−0.37		−0.69	
Cyclops bicuspidatus thomasi	0.03		NA		−0.08		0.85	
Mesocyclops edax	−0.07		NA		−0.05		NA	

*TABLE 7. Correlation (r) between alewife, bloater, and **Bythotrephes** abundances and Calanoida, Cyclopoida and Cladocera length and biomass (August only). Adults = age 1+. YOY = Young of Year. NA means that the organism was absent.*

	1983–92		1983–86		1987–92		1990–92	
	Adults	YOY	Adults	YOY	Adults	YOY	Adults	YOY
Alewife								
Length								
Calanoida adults	−0.46	−0.02	−0.96	−1.00	−0.10	0.26	1.00	0.91
Cladocera	−0.53	−0.57	0.84	0.94	−0.80	−0.68	−0.95	−0.98
Cyclopoida adults	0.02	0.06	−0.17	−0.38	0.16	−0.05	1.00	0.86
Biomass								
Calanoida	−0.12	−0.24	0.80	0.91	−0.05	−0.50	0.24	0.67
Cladocera	−0.39	−0.69	0.14	−0.08	−0.54	−0.74	−0.85	−1.00
Cyclopoida	0.09	−0.04	0.96	0.87	0.31	−0.26	0.98	0.78
Bloater								
Length								
Calanoida adults	0.15	0.68	0.99	0.94	0.61	0.69	0.95	0.90
Cladocera	−0.11	−0.29	−0.92	−1.00	−0.04	−0.51	−1.00	−0.98
Cyclopoida adults	0.66	0.24	0.33	0.71	0.84	0.31	0.90	0.84
Biomass								
Calanoida	−0.04	0.16	−0.89	−1.00	0.56	−0.36	0.59	0.69
Cladocera	−0.14	−0.50	0.02	0.46	−0.20	−0.78	−0.99	−1.00
Cyclopoida	−0.13	0.20	−0.90	−0.62	0.61	−0.16	0.83	0.76
Bythotrephes								
Length								
Calanoida adults	0.67		NA		0.74		0.95	
Cladocera	0.01		NA		−0.09		−1.00	
Cyclopoida adults	0.64		NA		0.57		0.90	
Biomass								
Calanoida	−0.02		NA		0.18		0.59	
Cladocera	−0.10		NA		−0.42		−0.99	
Cyclopoida	−0.21		NA		0.15		0.83	

TABLE 8. Average crustacean zooplankton biomass (mg/m^3 dry weight) for 1976 and 1984 to 1992, Lake Michigan. Values are the mean ± S.E. The 1976 data point (Bartone and Schelske 1982) is the average of April, May, July, and August values which were converted to dry weight (mg/m^3) assuming carbon content was 50% of dry weight. The 1984–1992 data represent the "unstratified spring" and "stratified summer (August only)" period only.

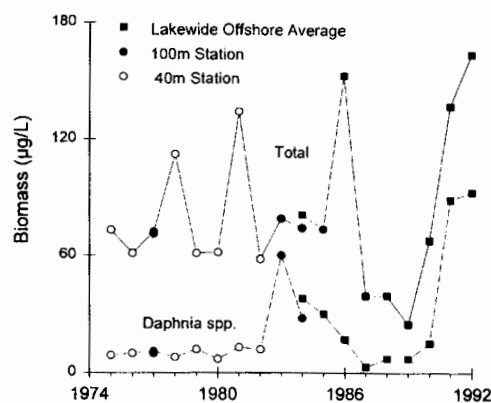|	
1976	50.0±14.8
1984	43.4± 9.0
1985	45.0± 6.9
1986	86.4±15.5
1987	21.5± 3.3
1988	24.9± 3.8
1989	20.0± 3.5
1990	38.6± 5.8
1991	51.7±22.0
1992	77.0±32.9

FIG. 6. Historical offshore zooplankton biomass trends in Lake Michigan during July and August. Data are from Scavia et al. (1986) and this study.

(Gannon *et al.* 1982, Stemberger and Evans 1984) although the species composition of nearshore and offshore populations has been similar.

Common rotifer species in the open waters of Lake Michigan during 1983–1992 included *Keratella cochlearis* and *Polyarthra vulgaris*, two species that were also reported as dominant or common in the offshore waters in 1930 (Ahlstrom 1936), and in the nearshore waters in 1926–27 (Eddy 1927), 1962 (Williams 1966), 1970 (Johnson 1972), and 1977 (Gannon *et al.* 1982). *Kellicottia longispina* was common in 1927, 1977, and 1983–1992. Since 1977, but not before, *Keratella crassa* and *Conochilus unicornis* (a colonial rotifer) also have been common.

Although the species of rotifers present in Lake Michigan has been consistent historically, their relative abundance has not. The three most abundant rotifer species during the period 1983–1987, *P. vulgaris*, *K. cochlearis*, and *Synchaeta* sp., were also among the four most abundant species during the period 1988–1992. However, during the latter 5 years, the abundance of these species was over 2.6 times that of the former period, and the most abundant species during 1988–1992, *C. unicornis*, was 15.2 times more abundant than during the previous 5 years. *Ploesoma truncatum* also became quite common during 1988–1992, following a sporadic presence during 1983–1987.

Crustacea

Although no intensive zooplankton studies of the offshore waters of the entire lake basin have taken place, some offshore studies of Lake Michigan zooplankton do exist. Wells (1960, 1970) sampled Crustacea with a number 2 (366 μm) net on four dates in June, July and August in 1954, 1966, and 1968 from the offshore region off Grand Haven, Michigan. On six dates (March 1969 to January 1970), Gannon (1975) collected crustaceans with a 64-μm mesh net from the offshore and inshore of Lake Michigan along a cross-lake transect from Milwaukee to Ludington. In September of 1973, northern Lake Michigan was sampled with a 250-μm mesh net (Schelske *et al.* 1976). Also, Stemberger and Evans (1984) provided abundance data (76-μm net) for a few zooplankters from offshore waters of the southeastern Lake Michigan area in 1979.

The data of Wells (1960, 1970) and Schelske *et al.* (1976) are useful but have to be used with caution. A 366-μm and a 250-μm net are probably

quantitative for larger crustaceans but certainly would not be for smaller crustaceans such as *Chydorus sphaericus, Bosmina longirostris, Eubosmina coregoni, Ceriodaphnia* spp., *Tropocyclops prasinus,* and copepods (Makarewicz and Likens 1979). Another difference between the data sets are the depths of collection. Wells (1969, 1970) sampled horizontally with a Clarke-Bumpus sampler at 10, 20, 30, and 40 m, while Schelske *et al.* (1976) sampled vertically from the bottom to the top.

The zooplankton populations in Lake Michigan underwent striking size-related changes between 1954 and 1966 (Wells 1970) similar to the 1990–1992 period. Species that declined sharply were the largest cladocerans (*Leptodora kindtii, Daphnia galeata mendotae,* and *D. retrocurva*), the largest calanoid copepods (*Limnocalanus macrurus, Epischura lacustris,* and *Diaptomus sicilis*) and the largest cyclopoid copepod (*Mesocyclops edax*). Medium-sized or small species (*D. longiremis, H. gibberum, Polyphemus pediculus, Bosmina longirostris, Ceriodaphnia spp., Cyclops bicuspidatus, Cyclops vernalis, Diaptomus ashlandi*) increased in number, probably in response to selective alewife predation on the larger organisms. After the alewife dieback, *M. edax* and *D. galeata mendotae* were still rare in 1968 when the composition of the zooplankton community shifted back toward one similar to 1954 (Wells 1970).

In northern Lake Michigan during September of 1973, predominant species were *Daphnia galeata mendotae, D. retrocurva, Limnocalanus macrurus, Diaptomus oregonensis, Eubosmina coregoni,* and *Diaptomus sicilis*. Cyclopoid copepods were a minor component of the fauna captured by a 250 μm net in 1973 (Schelske *et al.* 1976).

Cladocera

The changing nature of the zooplankton community of Lake Michigan (e.g., Scavia *et al.* 1986, Lehman 1991, Evans 1992) was evident by differences between our data for 1983 and that of earlier surveys (Table 9). *D. galeata mendotae* and *D. retrocurva* were the prominent daphnids in the 1954 study of Wells (1960). During the 1960s, *D. galeata mendotae* was rare, but *D. retrocurva* remained common with variable abundance. By 1983, *D. galeata mendotae* was again common, and they have remained so through 1992. *D. retrocurva* abundances were variable during 1983–1986, but then they became very rare in 1987 and subsequent years. In 1991 and 1992, *D. galeata mendotae*

TABLE 9. *Stratified summer (August only) Cladocera abundance in 1954, 1966, 1968, 1983 through 1992 in Lake Michigan. Data from Wells (1970) and this study. Values represent the mean station number/m³. Values in parentheses include Stations 6, 56, 64, and 77, which are nearshore sites not sampled after 1984. Length is the average length for the 1984–1992 period.*

Species	Length (mm)	1954	1966	1968	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
Bosmina longirostris	0.41	26	98	16	318 (342)	169 (5,231)	33	103	4,314	548	262	1,014	11	67
Bythotrephes cederstroemi	2.72	0	0	0	0	0	0	1	4	18	7	56	6	12
Ceriodaphnia quadrangula	0.65	0	4	1	0	0	0	0	0	0	0	0	0	0
Daphnia galeata	1.33	1,200	0	0.4	883 (514)	4,650 (3,508)	2,150	2,802	1,133	1,272	1,568	918	5,825	7,309
Daphnia longiremis	0.89	0	16	0	0	14	47	9	0	14	0	0	0	0
Daphnia pulicaria	1.39	0	0	0	2,447 (1,011)	303 (248)	694	396	0	0	0	9	0	0
Daphnia retrocurva	1.05	1,400	79	2,100	82 (82)	1,061 (1,061)	266	376	1	0	3	3	0	0
Diaphanosoma brachyurum	0.41	2	0	0	1	0	1	0	0	0	0	0	0	0
Eubosmina coregoni	0.51	0	1	16	80 (159)	202 (208)	66	100	0	1	51	12	0	0
Holopedium gibberum	0.87	0	2	5	23 (456)	66 (536)	8	70	0	0	0	7	0	0
Leptodora kindtii	4.43	29	4	16	42 (34)	66 (98)	43	71	8	2.5	0	0	0	0
Polyphemus pediculus	0.88	2	15	10	13	7	0	8	0	0.4	7	2	0	0
Total		2,659	219	2,164	3,889	6,538	3,308	3,936	5,460	1,856	1,898	2,021	5,842	7,388

abundance greatly increased while *D. retrocurva* were absent. The variation in abundance of another large cladoceran, *Leptodora kindtii*, was similar to that of *D. retrocurva*: about equally abundant in 1954 and 1983–1986, reduced abundance in the 1960s, and absent in our August samples since 1989. Lehman and Caceres (1993) did observe *Leptodora* in July of 1990, the last year of their study.

Most interesting is the appearance of the large daphnid *D. pulicaria* in the offshore region in the 1980s (Table 9). Evans and Jude (1986) reported that this species was first observed in Lake Michigan in 1978. Abundance remained low in southeastern Lake Michigan until 1982. In 1983, this species dominated the August *Daphnia* community both at the offshore stations of this study and at a station southwest of Grand Haven, Michigan. During 1984–1986, *D. pulicaria* were much less abundant than *D. galeata mendotae*, and by 1987, it had disappeared from the lake except for a few that were observed in 1990 (Table 9).

Another large cladoceran species was first identified in Lake Michigan in 1986, *Bythotrephes cederstroemi*. This organism preys on other zooplankton species, and it has been consistently present in August zooplankton collections from 1987 through 1992.

Smaller daphnids have also exhibited highly variable abundances year to year. The large increases in numbers of *Bosmina longirostris* and *Eubosmina coregoni* in 1983, compared to 1968, are probably due to smaller meshed nets being used for the 1983–1992 collections. From 1983–1992, *B. longirostris* was usually much more abundant than *E. coregoni*, with unusually large abundances in 1987 and 1990. Far fewer were collected in 1991 and 1992. *E. coregoni*, however, were rare or absent in 1987–1988 and again in 1991–1992.

In general, cladoceran diversity and equitability were greater during 1984 to 1986 than in later years (Table 10), although equitability remained high in 1987. More species were present with more similar biomass during the early 1980s, coincident with lowest predation pressure in ten years on zooplankton from the alewife (Fig. 4). After 1986, *B. cederstroemi* became established, alewife populations were larger than during 1983–1985, and large herbivorous cladocerans such as *H. gibberum*, *Leptodora kindtii*, *D. retrocurva*, and *D. pulicaria* became rare or absent. By 1991 and 1992, only three cladocera species were observed: the predator *B. cederstroemi*, the large *D. galeata mendotae*, and the diminutive *B. longirostris*.

TABLE 10. *Species diversity indices for Cladocera in Lake Michigan. N1 and E5 follow Hill (1973).*

	Species Diversity (N1)	Evenness (E5)
1984	2.92	0.58
1985	2.77	0.72
1986	3.99	0.70
1987	2.18	0.89
1988	1.64	0.46
1989	1.32	0.35
1990	2.11	0.50
1991	1.01	0.22
1992	1.01	0.26

Cladocera biomass was lowest in 1987, 2.2 μg/L, as compared to the 10 year average of 25.1 μg/L. In 1991 and 1992, however, 97.8 μg/L and 78.6 μg/L of cladoceran biomass, respectively, were observed due to the overwhelmingly dominant numbers of *D. galeata mendotae*.

Copepoda

Cyclops bicuspidatus was the dominant cyclopoid copepod during the 1983–92 period (Table 11). It reached its highest abundance in the mid-80s, decreased between 1987–1989, and increased to levels comparable to 1966 during 1990 to 1992.

Fewer *Mesocyclops edax* were found in August of 1983–87 than in 1954, another period of low alewife predation. However, abundance of this species had obviously increased since the 1960s, when they were not reported, and in the mid-1980s they appeared to be approaching levels similar to those observed in 1954. For example, abundance of *M. edax* in early October of 1983 reached a level comparable to 1954 (151 organisms/m^3, mean station abundance). However after 1985, abundance of *M. edax* decreased until 1990 when it was not observed (Table 11).

Tropocyclops prasinus mexicanus was not observed in the early works of Wells (1970). The large mesh net used in the earlier study undoubtedly missed this small cyclopoid.

Diaptomus ashlandi was the dominant calanoid copepod during 1983–1992. Its abundance was consistent year-to-year for the entire period 1983–1992 at levels 10 to 100 times those reported for 1954, 1966, or 1968. *Diaptomus minutus* appeared to
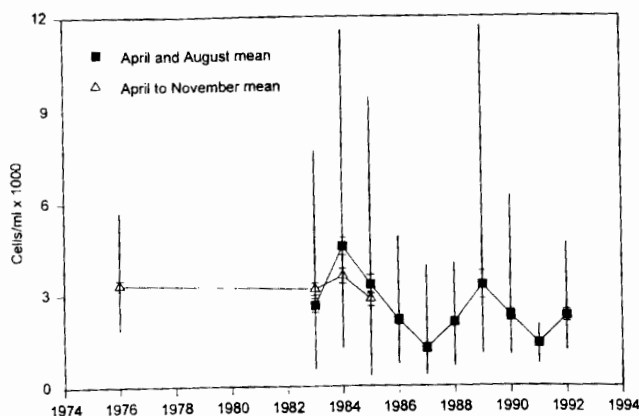
FIG. 7. Historical offshore epilimnetic phytoplankton abundance trends in Lake Michigan. Values are the mean ± S.E. (wide horizontal bar) and the range (narrow vertical bar). The 1976 data are from the Rockwell et al. (1980), while the 1983 to 1992 data are from Makarewicz et al. (1995). The 1983–92 phytoplankton data were collected at the same sites and times as the zooplankton data presented in this study.

ton were negatively correlated with alewife abundance, the correlational data generally suggest that alewife were not playing a strong role in affecting zooplankton biomass and length with the exception of size of the calanoid copepods (Table 7). The relaxation of alewife predation pressure probably played an important role allowing the establishment of *Bythotrephes cederstroemi* in the offshore waters of Lake Michigan in 1986. As in Lake Ontario, *Bythotrephes* appeared during a period of relaxation of alewife predation but were not observed in net samples after alewife abundance increased the following year (Makarewicz and Jones 1990). Correlational data suggested that adult and juvenile bloater chubs were negatively affecting Calanoida and Cyclopoida biomass and Cladocera length during the 1983–1986 period (Table 7).

1987–1992:
Bythotrephes Control or a Complex of Factors?

Wells (1970) observed that large-bodied *D. galeata mendotae* were lost during periods of strong alewife planktivory and that only the smaller *D. retrocurva* persisted when planktivorous fish increased in abundance. Daphnid species composi-

tions in 1986 and 1987 were exactly opposite to this pattern: *D. retrocurva* became rare and *D. galeata mendotae* became abundant. Considering this, and considering that the remaining *D. pulicaria* increased in size and only small individuals were taken, Lehman (1991) and Lehman and Caceres (1993) argued that the daphnid composition was consistent with invertebrate, rather than vertebrate, predation.

Also, some of the changes in species composition observed in this study could be due to indirect effects of *Bythotrephes* predation. For example, the loss of the predaceous *Leptodora* from Lake Michigan by *Bythotrephes* predation may have triggered further changes, including increased abundances of *Bosmina* and the colonial rotifer *Conochilus*, both of which are important prey items for *Leptodora* (Branstrator and Lehman 1991). Since 1986 and the introduction of *Bythotrephes*, abundance of *Leptodora* has decreased while *Conochilus* has increased dramatically. However, abundance of *Bosmina longirostris*, which did increase considerably for 1 year in 1987 after the establishment of *Bythotrephes*, has decreased to abundances similar to those observed in 1950s and 1960s when abundances of *Leptodora kindtii* were high (Table 9) which suggests control by another species. With the absence and lack of predation from *Leptodora* in the late 1980s and early 1990s, the decrease in *B. longirostris* and *Eubosmina coregoni* could be due to predation by other plankton feeders in the late 1980s and/or by competition for similar resources from *Daphnia* (Vanni 1986) which dominated the plankton community in Lake Michigan in the early 1990s.

Our lake-wide data not only support the contention that major changes in the *Daphnia* community occurred after the invasion of *B. cederstroemi* in 1986 but also that changes occurred in the abundance of several other species of Cladocera and one Cyclopoida. Subsequent to the establishment of *B. cederstroemi* in 1986, the relatively large, perhaps less mobile, herbivorous Cladocera (*D. pulicaria, D. retrocurva, Leptodora kindtii, Holopedium gibberum*) and the large cyclopoid *M. edax* decreased, abundance of the small Cladocera *Bosmina longirostris* was variable but increased (until 1991) compared to abundance in 1986 and the mean length of the Cladocera community dropped sharply from about 1.5 mm to less than 0.5 mm in 1 year from 1986 to 1987 (Fig. 8) suggesting the resurgence of a size-selective predator. Sprules *et al.* (1990) argued that since abundance of *Bosmina* increased and that of *Daphnia* decreased while
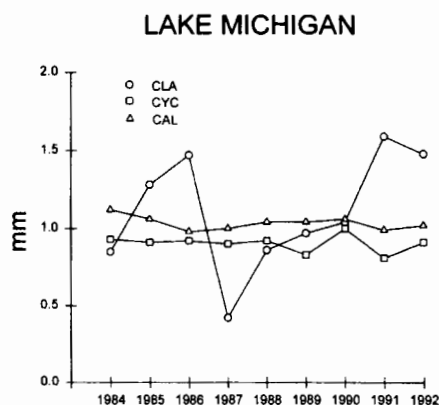
LAKE MICHIGAN

FIG. 8. Annual weighted mean length of Cladocera (CLA), Cyclopoida (CYC), and Calanoida (CAL) in Lake Michigan, 1983–92. For calanoid and cyclopoid copepods, copepodites and adults are included. **Bythotrephes cederstroemi** *is not included in the Cladocera.*

Bythotrephes cederstroemi abundance increased, predation by planktivorous fish was likely rather than by an invertebrate such as *Bythotrephes*. Not all large zooplankton species were reduced in number after 1987, however. The large calanoid *Epischura lacustris* had generally increased in abundance, and the abundances of the relatively large *Diaptomus minutus* (mean length = 0.90 mm), *D. sicilis* and *D. ashlandi* (mean length = 0.92 mm) were greater than those reported for 1954. The persistent occurrence of larger copepods in the presence of planktivorous fish does not necessarily invalidate a hypothesis of planktivorous fish predation affecting zooplankton species composition. It depends on the type of fish planktivory (i.e., obligate). For example, Rudstam *et al.* (1993) found little effect of planktivory by cisco and perch on calanoid copepods in Lake Mendota, Wisconsin, even though *Daphnia* were removed.

A major change in the species composition of Lake Michigan zooplankton was evident by 1990. By 1990, populations of other predaceous zooplankton such as the cladoceran *Leptodora* and the cyclopoid *Mesocyclops edax* were not observed in our lake-wide plankton samples. Abundances of smaller herbivorous Cladocera (*Bosmina longirostris* and *Eubosmina coregoni*) were variable through the 1980s, but they, too, sharply declined during 1991–1992. While there were 10 species of cladocerans in 1985, there were only three left by 1991, and in 1992 a single species (*D. galeata mendotae*) accounted for over 95% of the Cladocera abundance. Most of the herbivorous copepod species that were present during 1983–1985 remained abundant during 1991–1992. Is it possible that *Bythotrephes* is the sole cause of all the compositional changes in the pelagic zooplankton community of Lake Michigan observed, especially after 1990 when major changes in zooplankton composition occurred while *Bythotrephes* abundance was considerably lower than in 1989? We can not answer that question directly. However, has the abundance of other planktivorous organisms in the pelagic region of Lake Michigan increased?

Both alewife and the bloater chub (*Coregonus hoyi*) populations increased in 1987 over abundance levels of the previous year (Fig. 4). Adult alewife (over 1 year old) abundance in 1987 was 83% of the alewife population in 1981, a relatively high abundance year. Furthermore, young-of-the-year alewife were at the highest abundance in five years in 1987 (Fig. 5). Similarly, abundance of adult bloaters *Coregonus hoyi* (>1 year) were exceptionally high between 1987–1989 and 1992 (Fig. 4) but not young-of-the-year.

Not only do alewife feed on *B. cederstroemi* (Keilty 1990), but it is likely that the adult bloater will take *B. cederstroemi* since they readily feed on *Mysis* and *Leptodora* (Wells and Beeton 1963). In Lake Michigan, bloaters less than 20 mm in size fed selectively on cyclopoid copepods and above 35 mm in length on *Daphnia* (Warren and Lehman 1988). Bloaters switch to a benthic habitat and prey after one year among the pelagic zooplankton (Crowder and Crawford 1984). Dorazio *et al.* (1987) argued that changes in zooplankton composition and behavior observed in 1985 probably resulted from increased predation by visually oriented planktivorous fish such as the bloater. Our correlational data suggest that alewife (adults and juveniles) and juvenile bloaters were depressing Cladocera size and biomass, particularly larger species (Table 7) during the 1987–1992 period, while strong inverse correlations were not evident between zooplankton biomass and alewife, bloater or *Bythotrephes* abundance with the exception of *D. galeata mendotae*, *Diaptomus minutus*, and *D. sicilis* with juvenile alewife and juvenile bloater and *D. sicilis* and *D. galeata mendotae* with adult alewife.

During the 1990–1992 period, our correlational data suggest that all three zooplankton predators, including adult bloaters, were affecting abundance and size of zooplankton, especially Cladocera, in Lake

Michigan. It is possible that one or more predators other than *Bythotrephes cederstroemi* have been affecting the composition and abundance of zooplankton in Lake Michigan. Without stomach and gut content analysis from alewife, bloater and *Bythotrephes* from each year, the best that can be argued is that these planktivores either consecutively, starting with *Bythotrephes,* or simultaneously depressed cladoceran populations starting in 1987 and had a continued grazing pressure on cladocerans and some cyclopoids. These correlational analyses are limited by the fact that the fish trawl data represent only the bottom 1.8 m of the water column and the zooplankton data represent the top 20 m of the water column and do not consider vertical migration.

More recent data are needed on stomach content of bloaters from Lake Michigan. Even though the adult bloater population increased by a factor of 33% from 1986 to 1987, bloater are dismissed as the cause of the change in composition of the *Daphnia* populations because bloater were reported as changing from a pelagic to a benthic mode of feeding due to competition for food from alewife (Crowder and Crawford 1984). However, before the alewife presence in Lake Michigan, bloaters had been reported as pelagic zooplanktivores until age 3+, when they then began to switch to a bottom habitat and to benthic prey. Species of zooplankton present in bloater stomachs prior to alewife introduction include *Bosmina longirostris, Holopedium gibberum, Daphnia retrocurva, Daphnia galeata mendotae, Cyclops bicuspidatus,* etc. (Wells and Beeton 1963)—all zooplankton species whose abundance is currently changing in Lake Michigan. It is possible that with a depressed alewife population, the feeding behavior of adult bloater in Lake Michigan has changed.

Another question is what allows *Daphnia galeata mendotae* to increase in abundance in the face of a highly successful predator that has successfully eliminated several species of Cladocera? We do not have an answer to this. However, a similar situation was recently described in Lake Mendota (Rudstam *et al.* 1993). Three species of *Daphnia* were present in Lake Mendota: *Daphnia pulicaria, Daphnia galeata mendotae,* and *Daphnia retrocurva.* In the face of planktivory by a coregonid, the larger *Daphnia pulicaria* abundance was reduced, while the smaller *Daphnia galeata mendotae* abundance was marginally affected. The interyear changes in daphnid composition were explained by a combination of factors including differential planktivory, structure of the habitat, and

the physiological ecology of the dominant planktivore interacting with the competitive ability of the two species at different levels and temperature.

Food web model predictions based on functional or size-grouped components of Lake Michigan suggest that increased *Bythotrephes* abundance will cause Lake Michigan's plankton to return to a community similar to that of the 1970s with *Diaptomus* dominated zooplankton assemblage (Scavia *et al.* 1988). Such a change in zooplankton composition has occurred but not necessarily due solely to *Bythotrephes* predation; that alewife and bloater chub appear to have played a role in the change in species composition. Our data demonstrate that the composition and abundance of the calanoid community after 1987 are not unlike that of 1960s and that species diversity of the calanoid community is more diverse than the cladoceran community in the 1990s as compared to the early 1980s. Even though the relative biomass of the cladocerans has remained similar over the 1983–1992 period, the species diversity and evenness of the Cladocera community in the early 1990s is unlike anything that has been previously reported for Lake Michigan. Cladocera dominance is centered in one species, *Daphnia galeata mendotae,* and only three species of Cladocera were observed in the lake in 1991 and 1992.

ACKNOWLEDGMENTS

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